

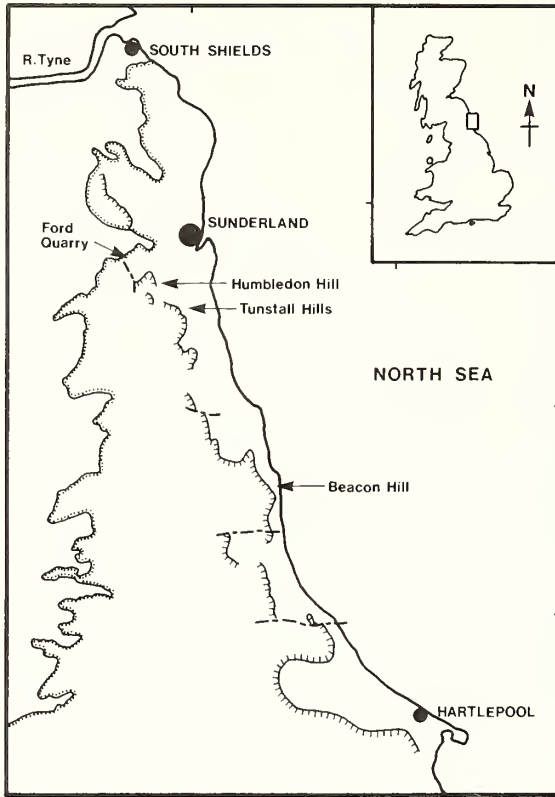
THE BRITISH PERMIAN CRINOID '*CYATHOCRINITES*' *RAMOSUS* (SCHLOTHEIM)

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ABSTRACT. Although dissociated ossicles are locally common in the Upper Permian, Zechstein Cycle 1, Ford Formation reef of north-east England, the crinoid fauna is monospecific, consisting of '*Cyathocrinites*' *ramosus* (Schlotheim). This species differs from *Cyathocrinites* s. s. in having a broad, bowl-shaped cup with wide radial arm facets and the right proximal plate of the anal tube incorporated into the calyx. The taxonomic position of '*C.*' *ramosus* below order level is uncertain. '*C.*' *ramosus* is interpreted as a rheophile and is found associated with a diverse fauna of mainly bivalves, gastropods, brachiopods, and bryozoans. A unique dorsal cup is known and dissociated ossicles from the crown and stem have been found, particularly the latter. The stem is xenomorphic. The proxistele was composed of low columnals and was particularly flexible. The mesistele was the principal organ of elevation of the crown. Dististele attachment was by a cirriferous runner. Two tentative palaeobiological deductions concerning the stem of '*C.*' *ramosus* are that the distinctive pentastellate jugula of the axial canal were possibly adaptations for efficient autotomy and that, if present, peripheral through-going ligaments may have been about seven to nine columnals in length.

IN his review of the Permo-Triassic extinction, Rhodes (1967) paid particular attention to the Crinoidea and noted that they were very diverse during the Permian, with over three hundred species having been described. So far only one species has been identified in the marine Upper Permian of north-east England (text-fig. 1), the cladid inadunate '*Cyathocrinites*' *ramosus* (Schlotheim); it was first recorded in Britain by King (1850) and forms part of the Permian reef fauna (text-figs. 1-3). Since King's description no re-evaluation of this taxon has been made. Although no further 'complete' dorsal cups have been found to supplement King's unique specimen, many dissociated ossicles have subsequently been collected. These are mainly columnals and pluricolumnals, both with and without cirri, but also include brachials, radials, and basals. The present reassessment of '*C.*' *ramosus* is based on this new material and King's original specimens.

Our study has confirmed that the British Upper Permian crinoid fauna is monospecific; such low diversity may be related to the restricted nature of the small 'inland sea' in which '*C.*' *ramosus* lived (Haszeldine 1984, fig. 6). This is in stark contrast to, say, the diverse crinoid faunas associated with reefs in the Lower Carboniferous of the UK and Ireland, when conditions were open marine (ibid., fig. 2) and quite unlike the relatively small basin, with (presumably) restricted circulation, in which the cyclic sediments of the Zechstein were deposited. This basin was connected to the open sea by a relatively narrow channel (ibid., fig. 6). These conditions may not have been particularly favourable for the migration of crinoids. The larvae of modern crinoids have a relatively short free-swimming period of from 5 to 108 hrs. (Breimer 1978). If currents into the basin were sluggish (as they are in the Mediterranean today, for example), conditions for the migration of larval crinoids would have been poor (although many modern crinoids, particularly the shallow water comatulids, have a wide distribution). However, the fact that one species did manage to colonize the basin indicates that migration was possible. Perhaps '*C.*' *ramosus* had some adaptive advantage over other contemporary crinoids which favoured life in an enclosed basin, but none has been deduced; quite similar cladid inadunates are found within the diverse crinoid faunas of the Lower Carboniferous in the UK and Ireland. '*C.*' *ramosus* may have had a particularly long living, free swimming larval stage which was able to colonize an enclosed basin. It is also possible that this species was relatively



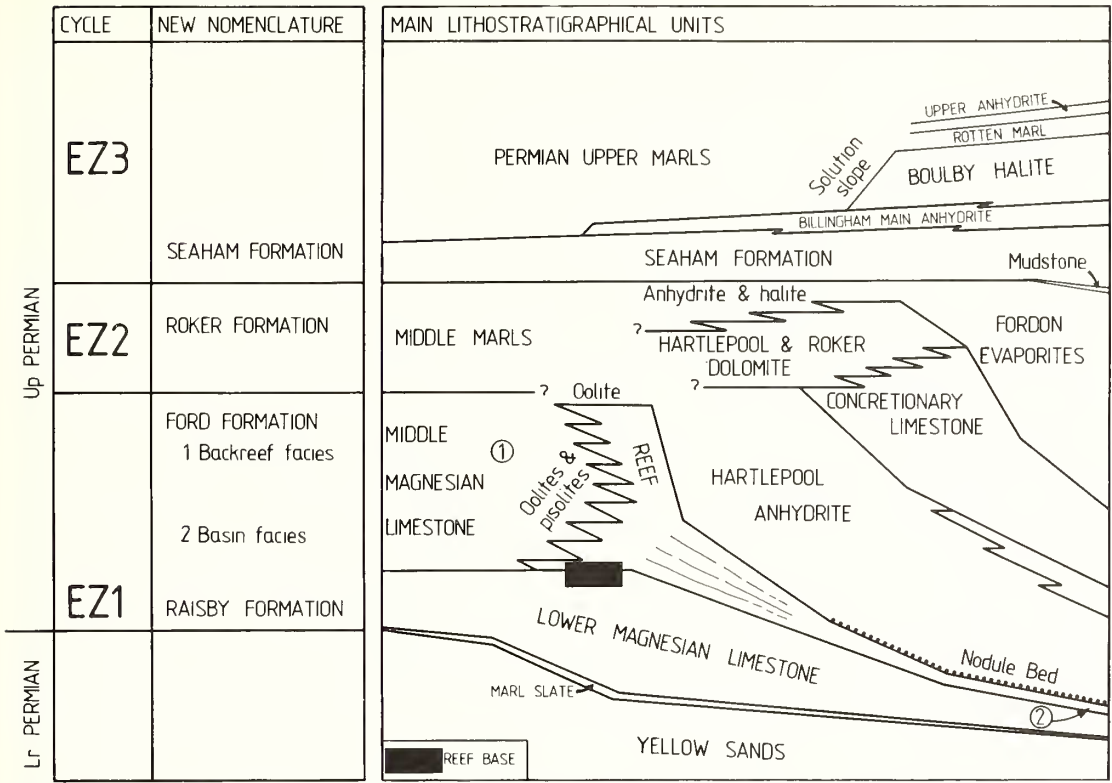
TEXT-FIG. 1. Outcrop of the Ford Formation reef facies (Zechstein Cycle 1, Upper Permian) in north-east England and the positions of localities mentioned in the text.

indifferent to changes in salinity which would have discouraged other crinoids. Such fluctuations in salinity would have occurred within even a small part of a single Zechstein cycle, for example, during a very dry summer.

STRATIGRAPHY

The Upper Permian of north-east England consists of a complex sequence of carbonates and evaporites which were deposited along the western margin of the Zechstein basin in five cycles (Smith 1980; Taylor 1984). Following the revision by Smith *et al.* (in press), a new stratigraphic nomenclature for the Zechstein is used herein (text-fig. 2).

Initial flooding of the Zechstein basin led to the deposition of the thin Marl Slate Formation (Cycle EZ1). This passes upwards into marine carbonates of the Raisby Formation, which was deposited in relatively deep water. The overlying Ford Formation comprises lagoonal and basinal deposits separated by a shelf edge reef which reaches a maximum thickness of 100 m. Lagoonal facies consist of cross bedded, oolitic, and pisolitic dolostones and dolomicrites. Widespread regression coupled with evaporative drawdown led to the termination of reef growth and deposition of the Hartlepool Anhydrite against the steep outer face of the reef. This evaporite thins basinwards into the North Sea.



TEXT-FIG. 2. Schematic stratigraphic cross-section and lithostratigraphic nomenclature of the Zechstein sequence in the Durham province (after Tucker and Hollingworth, in press; modified after Smith 1981).

The outcrop of the Ford Formation reef can be traced from north of Ford Quarry (text-fig. 1), through the western suburbs of Sunderland, and into County Durham, where it is known to extend a short distance south-west of Hartlepool, a total distance of about 32 km. Regional uplift has given the reef a gentle tilt to the south. Consequently, most of the main exposures of the reef base and lower reef core lithologies occur within the Borough of Sunderland. Southerly outcrops represent higher stratigraphic levels where a fuller reef profile is preserved.

PRESERVATION

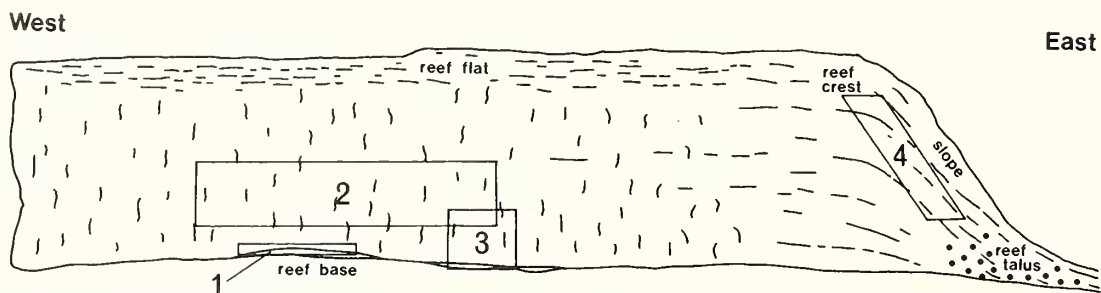
The Zechstein carbonates, and the Ford Formation reef in particular, have been subjected to extremes of diagenesis; fossils are generally poorly preserved, friable, and difficult to extract without causing damage, due to the almost complete pervasive dolomitization of the reef fabric. Some outcrops, however, such as the reef base at Tunstall Hill and small areas of Beacon Hill (text-fig. 1), are undolomitized and here fossils are generally well preserved. In particular, gastropods from the reef base such as *Naticopsis* have been found retaining original colour banding.

Living crinoids have an endoskeleton which alters from high-magnesium to low-magnesium calcite early in diagenesis. Porosity is also lost by the precipitation of epitaxial cement, so that columnals become large, single crystals of calcite. Crinoid ossicles in the Ford Formation are relatively well preserved, even in dolomitized lithologies, due to their subsequent resistance to diagenetic alteration.

PALAEOSYNECOLOGY

The Ford Formation reef contains a diverse and abundant fauna which displays a distinct faunal succession both laterally (in space) and vertically (in time) within different reef lithofacies. Similar faunal variations have been noted in Niagaran Reefs (late Silurian) by Walker and Alberstadt (1975). Although some taxa, such as the brachiopod *Dielasma*, are widely distributed throughout the reef, others, including '*C.* *ramosus*', are characteristic of certain lithologies, particularly those associated with the later stages of reef development.

The reef is founded in places upon a lenticular, shelly coquina or rudstone (Smith 1981) which contains a diverse fauna comprising: bivalves, such as *Bakevellia*, *Pseudomonotis*, *Liebea*, and *Schizodus*; brachiopods, including *Dielasma*, *Horridonia*, *Stenosisma*, and *Streptorhynchus*; abundant, usually fragmentary bryozoans, which include *Acanthocladia*, *Fenestella*, and *Dyscritella*; and gastropods, which form an important constituent of the reef base fauna and include *Mourlonia*, *Meekospira*, *Yummania*, and *Naticopsis*. Isolated ossicles and pluricolumnals of '*C.* *ramosus*' also occur but form a relatively minor constituent of the fauna. The coquina, where dolomitized, consists of shells which are tightly packed together in a sandy, dolomitic matrix (Smith 1981). Where the coquina is undolomitized (e.g. at Tunstall Hill; text-figs. 1, 3), bioclasts are coated by layers and fans of radiaxial fibrous calcite (Tucker and Hollingworth, in press).



TEXT-FIG. 3. The relation of crinoid bearing lithofacies to the Ford Formation reef facies (Zechstein Cycle 1, Upper Permian). 1, reef base, Tunstall Hill; 2, reef core, Tunstall Hill; 3, lower reef core, Humbledon Hill; 4, reef slope, Beacon Hill.

Petrographic evidence indicates that the coquina accumulated in a relatively shallow, warm, current agitated, normal marine environment with occasional and localized emergence. It is probable that the precipitation of inorganic cement between bioclasts, combined with the baffling and binding action of the bryozoan 'frameworks', led to the establishment and growth of the reef itself. Lower reef core lithologies tend to be numerically dominated by fenestrate and trepostome bryozoans, such as *Fenestella* and *Dyscritella*, and also display a wide degree of palaeocommunity overlap. '*C.* *ramosus*' occurs abundantly in lower reef core lithologies (text-fig. 3) where ossicles are often present in sufficient numbers to form crinoidal packstone lenses (e.g. at Humbledon Hill).

Distinct faunal communities evolved when the reef became fully established and was migrating rapidly basinwards over its own talus. In stratigraphically higher reef core lithologies crinoids become progressively rarer and are eventually confined to reef crest, slope, and talus areas (e.g. at Beacon Hill railway cutting, where the outcrops are representative of slope lithologies; text-fig. 3). This distribution pattern was probably due to environmental conditions remaining at an optimum in these areas.

SYSTEMATIC PALAEOONTOLOGY

Repositories of specimens. BMNH, British Museum (Natural History); SuM, Sunderland Museum; UCG, University College, Galway.

Terminology. Crinoid terminology follows Moore *et al.* (1968), Ubaghs (1978), and Webster (1974).

Class CRINOIDEA J. S. Miller, 1821

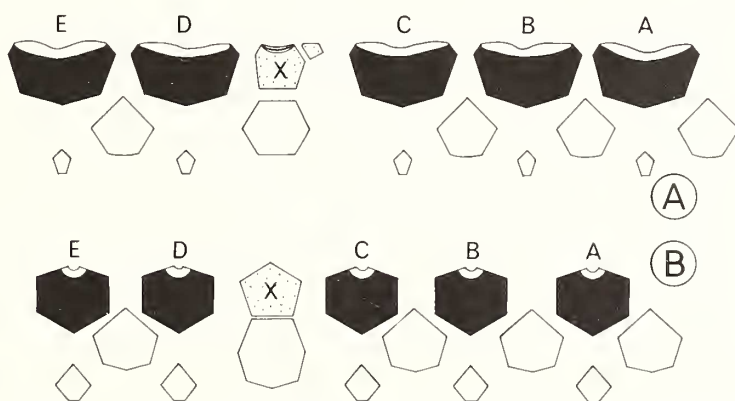
Subclass INADUNATA Wachsmuth and Springer, 1885

Order CLADIDA Moore and Laudon, 1943

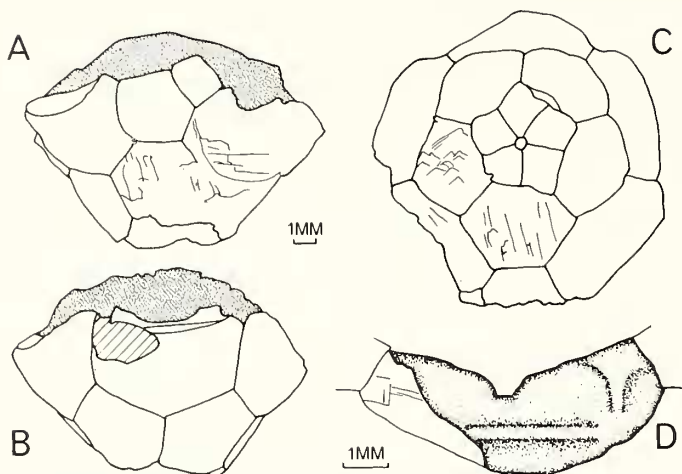
Incertae familiae

Discussion. '*Cyathocrinites*' *ramosus* differs from members of the genus *Cyathocrinites* in a number of important details. This is well illustrated by comparison with the type species *C. planus* Miller, 1821 (pp. 85–87, plates facing pp. 85 and 86). *C. planus* has a cup-shaped calyx, about as high as wide and steep sided. The arm articulation facets of radial plates are small, depressed, and semi-circular, and are situated in the most distal angle of each radial (text-fig. 4B). The outline of radial plates is approximately hexagonal. Only a single ossicle of the anal series, the anal X plate, is incorporated in the cup. In contrast, '*C.*' *ramosus* has a broad, bowl-shaped aboral cup (text-fig. 4A) with 'wing-like' radial plates which are wider than high (text-fig. 4A). Radials have very broad arm facets, corresponding to the longest side of the plate rather than an angle. Two ossicles of the anal series are incorporated in the calyx: the anal X plate and the right proximal plate of the anal tube (*sensu* Wright 1950, text-fig. 1). The latter ossicle is supported by X and the C-ray radial.

This combination of features indicates that '*C.*' *ramosus* is neither a member of the genus *Cyathocrinites* nor indeed the family Cyathocrinitidae, as they are at present understood, despite King (1850, pp. 50–51) erroneously placing *C. planus* and '*C.*' *ramosus* in synonymy. The aboral cup of '*C.*' *ramosus* does bear a superficial resemblance to that of the cyathocrinitacean *Barycrinus* (Moore *et al.* 1978, p. T580, fig. 372.2), which is also broadly bowl-shaped with wide radials and elongate arm facets on the radial plates. However, *Barycrinus* incorporates only a single anal plate (X) in the calyx and a radianal is present (absent in '*C.*' *ramosus*). *Barycrinus* is also somewhat unusual, and very distinctive, in being an Upper Palaeozoic inadunate with a pentameric stem. The column of '*C.*' *ramosus* is certainly holomeric.



TEXT-FIG. 4. Schematic diagrams of cup plating in cladid inadunate crinoids. A, '*Cyathocrinites*' *ramosus* (Schlotheim). B, *Cyathocrinites*, based on the type species *C. planus* Miller, 1821. Basals and infrabasals unshaded; radials black (with unshaded articular facets); plates of the anal series stippled; X, anal X plate. Shading scheme after Moore (1962).



TEXT-FIG. 5. '*Cyathocrinites*' *ramosus* (Schlotheim), UCG C26a, camera lucida drawings of the dorsal cup. A, lateral view with CD interray central. B, lateral view with A ray central. C, base with lumen surrounded by infrabasals central and A ray top. D, articular facet of A ray radial.

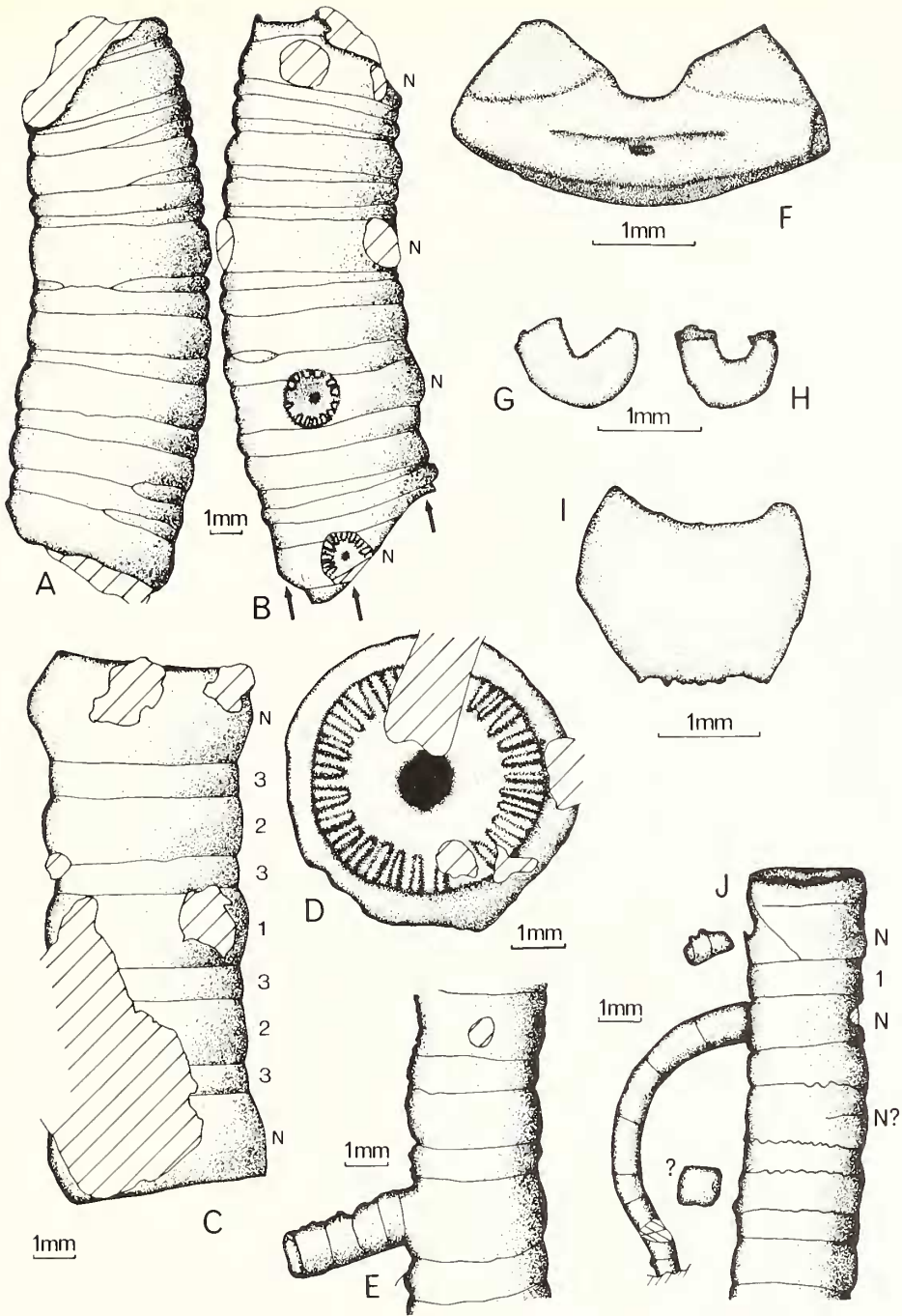
The only available cup of '*C.*' *ramosus* most closely resembles that of an advanced poteriocrinine inadunate but is not sufficiently well preserved to enable a generic identification. The precise taxonomic position of '*C.*' *ramosus* is therefore indeterminate.

'Cyathocrinites' ramosus (Schlotheim, 1816-1817)

Plates 71 and 72; text-figs. 4A, 5, 6, 9

- 1816-1817 *Encrinites ramosus* Schlotheim, p. 20, pl. 2, fig. 8; pl. 3.
 1820 *Encrinites ramosus* Schlotheim; Schlotheim, p. 20, pl. 2, fig. 8; pl. 3, fig. 19a, b.
 1848 *Cyathocrinus ramosus* (Schlotheim); Geinitz, p. 16, pl. 7, figs. 3-6.
 1848 *Encrinites planus* Miller; Howse, p. 259.
 1850 *Cyathocrinus ramosus* Schlotheim; King, pp. 50-52, pl. 6, figs. 15-20.
 1861 *Cyathocrinus ramosus* (Schlotheim); Geinitz, p. 109, pl. 20, figs. 10-14.
 1866 *Cyathocrinus ramosus* (Schlotheim); Geinitz, p. 62, pl. 4, fig. 19.
 1894 *Cyathocrinus ramosus* (Schlotheim); Netschajew, p. 116, pl. 1, figs 4, 5.
 1898 *Cyathocrinus ramosus* (Schlotheim); Spandel, p. 28, pl. 12, figs. 1-4, 8-20.
 1913 *Cyathocrinus ramosus* (Schlotheim); Trechmann, p. 215.
 1943 *Cyathocrinites ramosus* Schlotheim; Bassler and Moodey, p. 120.
 1943 *Cyathocrinites* (?) *ramosus* (Schlotheim); Bassler and Moodey, p. 395.
 1943 *Cyathocrinus ramosus* (Schlotheim); Trechmann, p. 343.
 1948 *Cyathocrinus ramosus* (Schlotheim); Branson, p. 189.
 1967 crinoid columnals; Smith and Francis, p. 178.
 1977 *Cyathocrinites ramosus* (Schlotheim); Pattison, p. 44.
 1980 *Cyathocrinites* sp.; Pettigrew, p. 18.

Material, horizon, and localities (text-fig. 1). King's original specimens are numbered UCG C26a-g. The unique dorsal cup is UCG C26a; all other specimens are pluricolumnals. UCG ?C27 is a poorly preserved pluricolumnal for which a definite identification is impossible. All of this material comes from Tunstall Hill, Sunderland, Tyne and Wear (NGR NZ391544, approximately). Column material in the collection of Sunderland Museum (SuM) comes from three localities: SuM B2769 (fifty-four specimens) from Ford Quarry (NGR NZ362572); SuM B2770 (106 specimens) from Tunstall Hill; and SuM B2772 (twenty-two specimens)



TEXT-FIG. 6. '*Cyathocrinites*' *ramosus* (Schlottheim), camera lucida drawings of pluricolumnals and dissociated ossicles from Tunstall Hill (A-E) and Beacon Hill (F-J). A, B, BMNH E70126, lateral views of a pluricolumnal from opposite sides, showing wedge-shaped tertinternodals which contribute to the curvature of the specimen and cirrus scars arranged in three rows (indicated by arrows), although no cirrinodal bears three scars. C, D, BMNH E70127, a pluricolumnal from the mesistele; C, lateral view, showing regular arrangement of columnals (N3231323N) and nudinodals; D, articular facet and convex latus of a nodal. E, BMNH E70128, part of a pluricolumnal, with a cirrus arising from a cirrinodal at a slight angle (noditaxis arrangement N212). F, BMNH E70138, articular facet of a radial plate (cf. text-fig. 5D). G, H, BMNH E70130, E70132 respectively, brachial ossicles. I, BMNH E70129, CD interarray basal. J, BMNH E70134, pluricolumnal with strongly curved cirrus and (apparently) tall cirral ossicles.

from Humbledon Hill (NGR NZ380552). New material has been collected by Hollingworth and Donovan from Tunstall Hill (BMNH E70126–E70128) and Beacon Hill railway cutting near Seaham (BMNH E70129–E70172; NGR NZ441455). All of these localities are within the Ford Formation reef facies (see above), Zechstein Cycle 1, Upper Permian. We have been unable to trace Schlotheim's original material.

Diagnosis. A species of cladid inadunate crinoid with a broad, bowl-shaped calyx which tapers to a relatively narrow base. Infrabasals and basals pentagonal, except for the basal in the CD interray, which is hexagonal. Radials broader than high, elongate heptagonal in outline, with elongate arm articulation facets. Anal X and the right proximal plate of the anal tube incorporated in the CD interray of the calyx, the latter supported by the C-ray radial and X. Arms unknown but brachials were broad proximally, becoming narrower and more U-shaped distally. Column circular to pentagonal in outline with a central, pentagonal axial canal with pentastellate jugula. Columnals have marginal crenularia and circular areolae. Stem xenomorphic, with a proxistele composed of numerous low columnals, a mesistele of taller columnals which lack cirri and a cirriferous dististele with a maximum of three cirrus scars per cirrinodal. Attachment was by cirriferous runner.

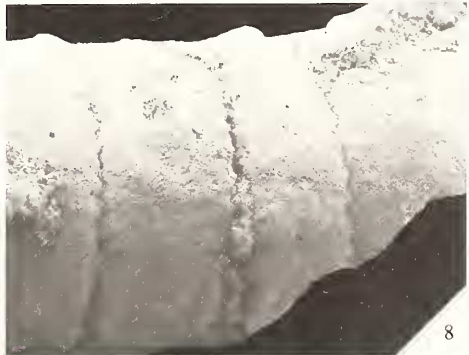
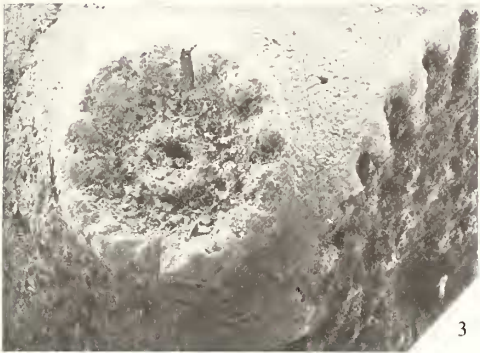
Description. The arms are unknown apart from dissociated brachials. King (1850, p. 51) noted, 'I have not yet succeeded in procuring any specimens of the arms or branches of *Cyathocrinus ramosus*; though single joints have now and then occurred to me'. Two poorly preserved brachials have been collected from Beacon Hill by Donovan (text-fig. 6G, H). These are approximately semicircular in outline with a V- or U-shaped adoral food groove and apparently synostosal articulation (probably due to poor preservation). Such brachials are not suited to articulate on the radial facet (text-figs. 5D, 6F) and are, therefore, derived from a more distal part of the arm. The 1Br₁ would have been somewhat broader, with a symplectial fulcral ridge parallel to the oral surface and an elliptical lumen aboral to this ridge. The lumen position indicates that the flexure of this articulation was principally away from the oral surface. The pattern of arm branching is unknown.

The calyx is broad, conical, and tapers towards the base (text-figs. 4A, 5, 6F, 1); dicyclic. Five elongate, pentagonal infrabasal plates (text-figs. 4A, 5C) which were presumably visible in lateral view (in UCG C26a all five infrabasals are damaged, possibly due to mechanical damage after the cup had been glued to a board for display). Infrabasal plates and angles of the small, pentagonal lumen are radial in position. The stem articulation facet at the base of the cup is unknown. Five basal plates with slightly convex lateral surfaces (text-fig. 5A, B). Basal in CD interray hexagonal (text-figs. 5A, 6i), other basals pentagonal. Each basal supported by the two adjacent infrabasals (text-figs. 4A, 5A–C). Five broad, heptagonal radial plates, all slightly convex. Arm facets broad, 'banana-like', with a narrow, central, adoral food groove. A synarthrial articulation ridge lies parallel to the long axis of each facet but slightly aboral in position. An elliptical lumen is situated aborally to the fulcral ridge. Two short ridges, one at each end of the facet, are perpendicular to the fulcral ridge (text-figs. 5D, 6F). Lateral surfaces of radials and basals unsculptured. Anal X approximately pentagonal. Small, tetragonal right proximal plate of anal tube supported by X and C-ray radial.

Stem fragments of this species are common fossils at certain localities and, following examination of over 300 specimens, it is confidently recognized that the column was xenomorphic and divided into three distinct regions (text-fig. 9). The proxistele is composed of very numerous low columnals of varying diameter. SuM B2770/11 (Pl. 72, fig. 1) is a pluricolumnal from the proxistele formed of more than fifteen ossicles, either

EXPLANATION OF PLATE 71

Figs. 1–8. '*Cyathocrinites*' *ramosus* (Schlotheim). Tunstall Hill, Sunderland (except fig. 7); Ford Formation reef facies, Zechstein Cycle 1, Upper Permian. Scanning electron micrographs of features of the stem. 1 and 2, SuM B2770/9; 1, articular facet with a well-preserved pentastellate jugulum within the pentagonal lumen, $\times 11.5$; 2, enlargement of the lumen to show the jugulum, $\times 23$. 3, SuM B2770/18, cirrus scar with well-preserved crenularium and perilumen in depressed areola, $\times 23$. 4, SuM B2770/13, pluricolumnal with disc-like juvenile attachment(?) extending over three columnals (including a cirrinodal, left), $\times 11.5$. 5, SuM B2770/23, nodal with incipient cirrus scar, $\times 48$. 6, SuM B2770/27, angled cirrus scars on cirrinodal, the upper scar retaining a wedge-shaped cirral ossicle (cf. Pl. 72, fig. 5), $\times 11.5$. 7, SuM B2772/8, Humbledon Hill, Sunderland; cirral ossicle encroaching onto internodal adjacent to cirrinodal (note that the second cirrus scar is perpendicular, not angled, to the long axis of the column), $\times 9$. 8, SuM B2770/20, pluricolumnal which is slightly curved due to a wedge-shaped columnal (centre), $\times 11.5$.



N3231323 or N434243414342434(?). The nodals in this region are non-cirriforous. Latera convex, with either a 'knobbly' sculpture or unsculptured. Some columnals of the proxistele have raised rims which surround the articular facet. SuM B2770/19 (Pl. 72, fig. 2) is from a more distal part of the proxistele, with a general increase in nodal height.

The mesistele is composed of taller columnals than the proxistele, with planar or convex, unsculptured latera, and a columnal arrangement N3231323 (text-fig. 6c; possibly also N1, N212 in some stems). Nodals in this region do not bear cirri (at least proximally) but what appear to be incipient cirrus scars are apparent on some nodals as depressed, circular grooves (Pl. 71, fig. 5) or small pores (canaliculi). The ossicle enclosed by the circular groove probably develops into the distal primary cirral ossicle (Donovan 1984).

The dististele is similar to the mesistele but nodals are usually cirriforous. Nodals in this region bear from zero to three cirrus scars (Pl. 71, figs. 3, 4, 6, 7; Pl. 72, figs. 3-5; text-fig. 6A, B, E, J). Cirrinodal height varies within single pluricolumnals. Cirrus scars are generally at 72° to each other and arranged in columns on the latera (arrowed in text-fig. 6b). Cirrus scars rarely extend onto adjacent internodals and may be flush with the latera, depressed within a raised cone (Pl. 71, fig. 3), or angled towards the long axis of the stem (Pl. 71, fig. 6; the direction of angling is consistent within pluricolumnals but it is not known if this was towards or away from the crown; both orientations are found in isocrinids but are not mixed in any species). Curvature of the dististele is sometimes aided by wedge-shaped tert- and quartinternodals (Pl. 71, fig. 8; text-fig. 6A, B).

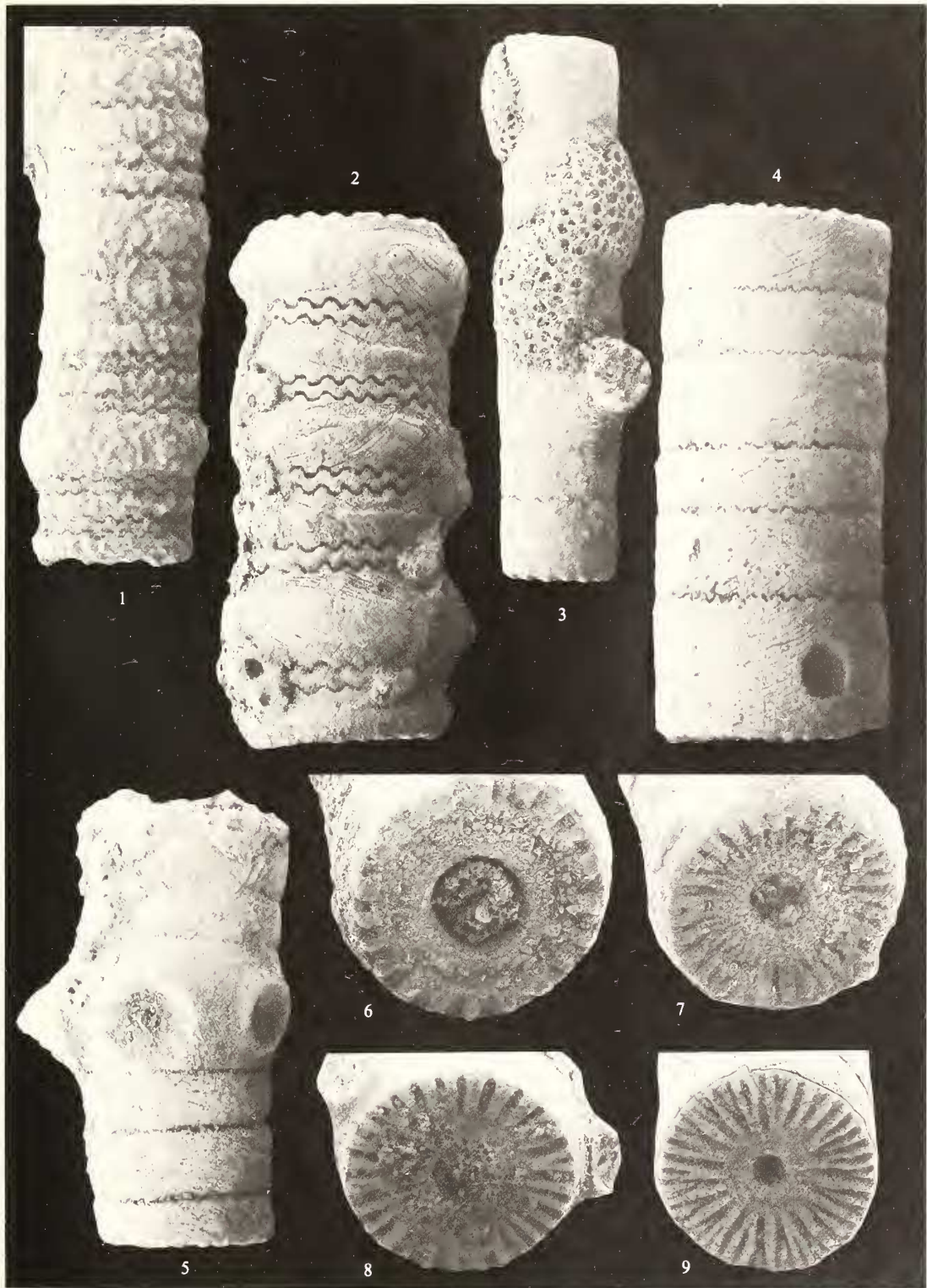
Columnals are either circular (sometimes slightly elliptical, due to poor preservation in the majority of examples) or pentagonal with rounded angles. Latera are planar or convex. Articular facets are either circular or rounded pentagonal in outline (Pl. 71, fig. 1; Pl. 72, figs. 6-9). The lumen is central, pentagonal (sometimes appearing circular although this is due to poor preservation in many, if not all examples; text-fig. 6D), with the angles of the column and axial canal coincident. In exceptionally well-preserved specimens a pentastellate jugulum is seen, produced by claustra which slope towards the centre of the axial canal (Pl. 71, figs. 1 and 2). The lumen is often surrounded by a narrow perilumen of irregular ridges and grooves (Pl. 71, figs. 1 and 2) which in turn lies within a slightly depressed, circular areola (Pl. 71, fig. 1; Pl. 72, figs. 6-9; text-fig. 6D). Articulation is symplexial with marginal, radial crenularia showing a limited range of morphological variation. At first crenulae are short, peglike, and unbranched (Pl. 72, fig. 6; text-fig. 6D). On a few specimens fine, paired ridges are seen to extend into the areola (Pl. 72, fig. 7), which is perhaps a prelude to the culmina becoming longer and extending towards the lumen (Pl. 72, fig. 8). These culmina show some slight bifurcation at the circumference of the facet. Further growth of the culmina, possibly related to an increase in columnal diameter, leads to increased bifurcation and implantation (Pl. 72, fig. 9; Moore 1939, p. 184, fig. 4) until separation of branched crenulae occurs. In addition, some of the columnal-columnal articulations are curved (e.g. SuM 2769/4, where KH(N) varies from 1.9 mm to 2.0 mm).

Bivariate analysis of columnals and pluricolumnals from the collection of Sunderland Museum (text-fig. 7) enabled calculation of the following equations which define the nodal in '*C.* ramosus' (symbols explained in the caption to text-fig. 7): $FD = 6.0KH - 7.9 = 7.4LD - 1.6 = 0.2C_n - 2.0$.

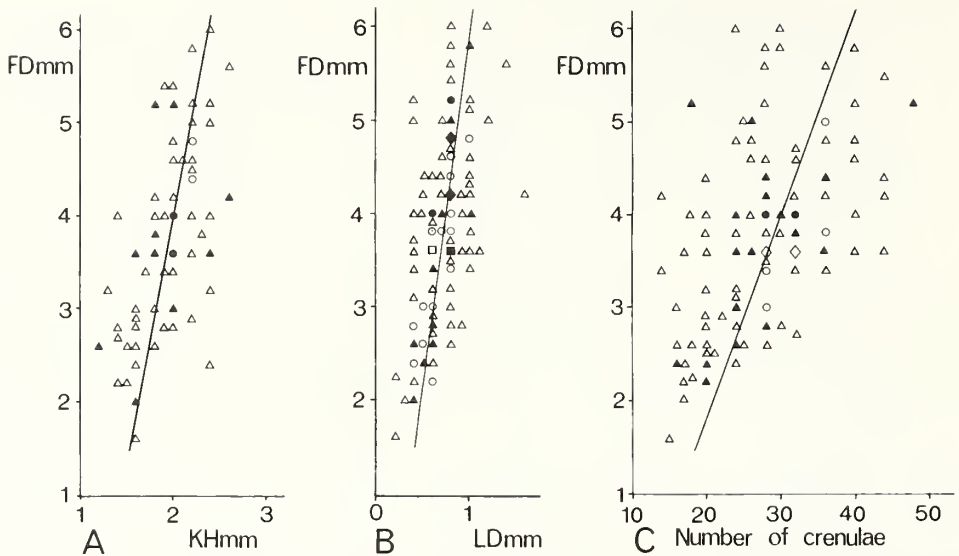
Cirri arise from the nodals (cirrinodals) of the dististele (and possibly also the distal part of the mesistele). The distribution of cirrus scars is discussed above. The articular facet sculpture of cirrus scars and cirral ossicles is similar to that of columnals. However, cirrus scars are sometimes concave and the crenulae of both scars and cirral ossicles do not bifurcate (Pl. 71, figs. 3, 6, 7). Cirral ossicles are also much smaller than columnals. The axial canal outline in cirri is indistinct but may be circular. In rare examples the cirral ossicle

EXPLANATION OF PLATE 72

Figs. 1-9. '*Cyathocrinites*' ramosus (Schlotheim). Tunstall Hill, Sunderland; Ford Formation reef facies, Zechstein Cycle 1, Upper Permian. Scanning electron micrographs of features of the stem. 1-5, pluricolumnals in lateral view; 1, SuM B2770/11, part of the proxistele (note that columnals are generally low, with obvious symplexial articulations between columnals and no cirrus scars on nodals), $\times 9.5$; 2, SuM B2770/19, a pluricolumnal from a slightly more distal part of the stem, $\times 12$; 3, SuM B2770/48, part of the dististele encrusted by the bryozoan *Dyscritella* sp., $\times 12$; 4, SuM B2770/4, a more robust pluricolumnal from a dististele, $\times 10$; 5, SuM B2770/27, part of the dististele, including a cirrinodal with three cirrus scars (cf. Pl. 71, fig. 6), $\times 8$. 6-9, sequence of articular facets showing the probable pattern of crenularium growth; 6, SuM B2770/23, marginal crenularium of short, peg-like culmina, $\times 14$; 7, SuM B2770/79, fine paired ridges extend from the culmina towards the lumen, $\times 12.5$; 8, SuM B2770/18, lengthening of culmina towards lumen, $\times 10$; 9, SuM B2770/4, facet with branching and secondary culmina, $\times 10$.



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TEXT-FIG. 7. Graphs plotted from measurements of *Cyathocrinites ramosus* (Schlotheim) taken from specimens in Sunderland Museum. A, facet diameter (FD) against nodal height (KH); $FD = 6.0KH - 7.9$. B, FD against lumen diameter (LD); $FD = 7.4LD - 1.6$. C, FD against number of crenulae per facet (C_n); $FD = 0.2C_n - 2.0$. Lines of best fit determined by Bartlett's method (Fryer 1966).

adjacent to the cirrus scar is wedge-shaped (Pl. 71, fig. 6) and very infrequently encroaches on the adjacent internodal (Pl. 71, fig. 7). Cirri vary from straight (text-fig. 6E) to highly curved (text-fig. 6J); the latter example seems to have very tall cirral ossicles but they are usually broader than high and homeomorphic (?). A cirrus on BMNH E70138 is 45 mm long but incomplete, approximately straight but slightly sinuous; for comparison, the longest pluricolumnal (on BMNH E70128) is 68 mm long.

The attachment disc of one juvenile has been identified (Pl. 71, fig. 4).

Discussion. Although only a single complete dorsal cup of *C. ramosus* is known from the Upper Permian of north-east England, pluricolumnals and columnals are plentiful. Dissociated plates from the crown are also known. The constancy of morphology shown by stem fragments indicates that only a single species of crinoid is present and, in consequence, all cup, arm, and column material are related with confidence. Peculiarities exist but these are rare and can be explained as being due to poor preservation. For example, two columnals on BMNH E70139 have a subsemicircular section which is reminiscent of the stem in myelodactylid inadunates. However, weathering has emphasized the growth lines, which are concentric, circular, and truncated against the flattened surface. It is concluded that these columnals were originally circular in outline but have had one side flattened, probably by weathering or pressure solution. Both are possibly derived from the same pluricolumnal.

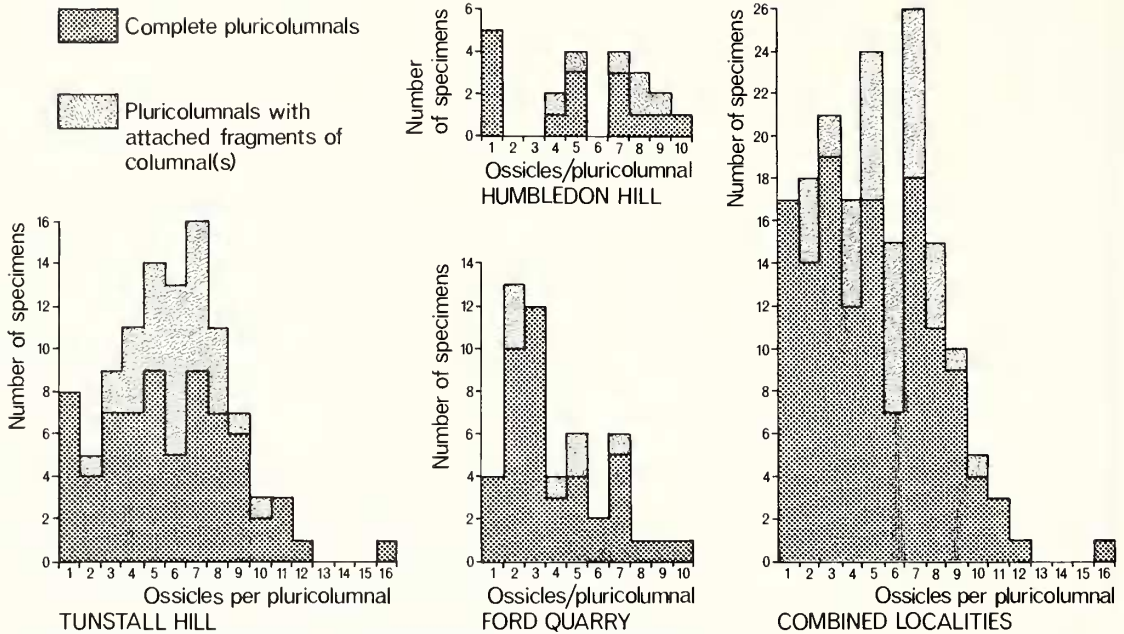
C. ramosus differs from a modern isocrinid in not having regularly spaced, synostosially articulating columnals (cf. Donovan 1984). In modern isocrinids synostoses occur between each nodal of the dististele and the adjacent distal internodal, called the infranodal (Breimer 1978, p. T24, fig. 11). These are the preferred zones of autotomy in the isocrinid stem (Emson and Wilkie 1980, pp. 200–201). There are no preferred autotomy surfaces apparent in the stem of *C. ramosus*. Indeed, there is no direct evidence that Palaeozoic crinoids were able to autotomize. However, any functional examination that we make of an ancient crinoid must be prejudiced by our knowledge of recent, stemmed crinoids, particularly isocrinids. There are two conflicting conclusions that may be drawn from the absence of definite autotomy surfaces in the stem of *C. ramosus*. Obviously, it may be

that the stem of '*C.*' *ramosus* was incapable of autotomy. On the basis of our interpretation of certain structures discussed below, however, it is tentatively proposed that the capability for self mutilation in '*C.*' *ramosus* was evenly distributed throughout the column, or perhaps just within the dististele. This is problematic in that it requires every columnal to have the ability to adopt the role of terminal ossicle, should autotomy occur at its distal facet. In modern isocrinids such as *Neocrinus decorus* this only applies to nodal ossicles, which have an axial canal unlike other columnals in the stem (Donovan 1984, p. 836, pl. 74, fig. 3). This canal is constricted by spicules of calcite which presumably grow rapidly after autotomy to seal the distal lumen. Grimmer, *et al.* (1985, p. 44) have also proposed that the spicules act as anchors for the soft tissues of the axial canal, preventing them from being torn out during autotomy.

We propose that the pentastellate jugula in '*C.*' *ramosus* (Pl. 71, figs. 1 and 2) may have acted in a similar manner to the spicules of isocrinids. The jugulum could have fulfilled an anchoring function for soft tissue while being able to rapidly infill by precipitation of calcite. It is intuitively obvious that a pentastellate canal could become infilled more rapidly than a pentagonal canal of identical area. The frequency of pentastellate jugula in columnals of '*C.*' *ramosus* is unknown but is certainly not a feature which is confined to nodals. It is perhaps too delicate a structure for frequent preservation and is probably often obscured by sediment. We postulate that every columnal in the dististele, and possibly also the mesistele, had a pentastellate jugulum. It is recognized that the soft tissues of the axial canal would also need to show the same frequency of 'segmentation' as the columnals of the stem in order to make autotomy possible at every columnal-columnal articulation.

Bivariate analyses of stem material were made using the collections from Sunderland Museum. These columnals were generally well preserved and come from three quarries which represent the reef core lithology. (The collection of material from Beacon Hill, now in the BMNH, is large but preservation is poorer, with pluricolumnals often broken or partly obscured.) The Sunderland Museum material has also been used in an analysis of pluricolumnal length (text-fig. 8). Grimmer *et al.* (1985) recognized three ligament types in the isocrinid stem: intercolumnal ligaments at synostosomal articulations; intercolumnal ligaments at symplexial articulations, which only insert at the crenulae; and peripheral through-going ligaments, which are limited to the areola and include about a dozen columnals each. By analogy, the latter two ligament types may have been present in '*C.*' *ramosus*; it might be possible to determine the length of the peripheral through-going ligaments in this species (if present) by examination of the number of columnals per pluricolumnal, assuming that these long fibres had some influence on the pattern of post-mortem stem disarticulation. Independent support for this hypothesis is not given by the stereom microstructure of the areola, which is at best very poorly preserved. Simple bar graphs of number of specimens against ossicles per pluricolumnal have been plotted for Tunstall Hill, Ford Quarry, and Humbledon Hill, both separately and combined (text-fig. 8). Unfortunately it is not known what form collecting bias takes in these samples, although more single, dissociated columnals might be expected, as well as some longer pluricolumnals. For example, BMNH E70126 (text-fig. 6A, B) has twenty-three columnals. Also, slightly different environmental conditions, rates of burial, and rates of cementation at these localities probably had some effect. Examination of the graphs of Tunstall Hill, Ford Quarry, and the combined localities (Humbledon Hill is ignored as a separate sample because of the small number of specimens) indicates a decrease in pluricolumnal number after the seven to nine columnal region; this may be due to peripheral through-going ligaments reaching such a maximum length. However, some mechanical constraint on pluricolumnal length cannot be discounted. Although the calculated 'ligament lengths' correspond approximately to internoditaxes 3231323 and noditaxes N3231323, other seven to nine ossicle pluricolumnals are also common.

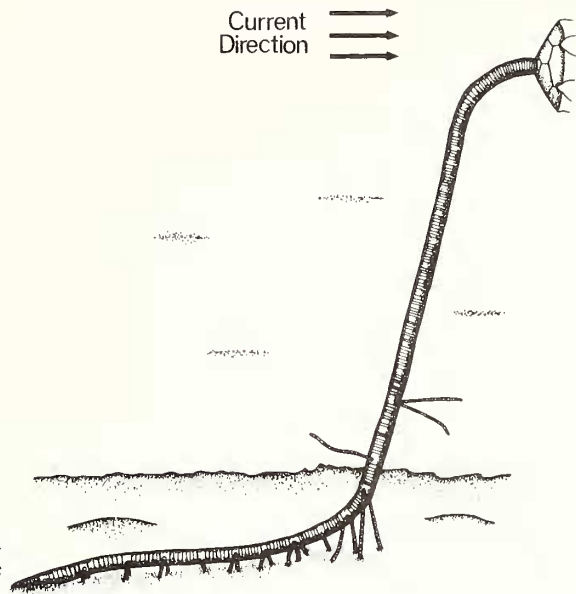
Epifaunal elements associated with pluricolumnals of '*C.*' *ramosus* include the bryozoan *Dyscritella* sp. (Pl. 72, fig. 3) and a possible juvenile attachment structure (Pl. 71, fig. 4) but no borings. There is no evidence that these encrustations occurred during the life of the crinoid. Indeed, confirmation of post-mortem encrustation is shown by SuM B2770/68, in which *Dyscritella* sp. has grown over an articular facet. Some plates on the calyx UCG C26a show signs of possible encrustation by epizoans.



TEXT-FIG. 8. Bar graphs showing the variation in pluricolumnal length, with respect to number of columnals, for specimens of '*Cyathocrinites*' *ramosus* (Schlotheim) in Sunderland Museum. Number of specimens against ossicles per pluricolumnal are plotted for Tunstall Hill (N = 102, mode = 7, mean = 6), Humbledon Hill (N = 21, mode = 1, mean = 5), Ford Quarry (N = 50, mode = 2, mean = 4), and combined localities (N = 173, mode = 7, mean = 5).

In the absence of a crown, the arm facets of radial plates are of particular importance in deducing the relationship of the arms to the cup. The radial arm facets (text-figs. 5D, 6F) of the British Permian species each have a longitudinal synarthrial articulation ridge which would have permitted an arm to 'rock' about an axis parallel to a tangent to the circumference of the cup in the radial position. The axial canal of the arm facet does not lie in the centre of the articular ridge but between the ridge and the aboral margin. This would probably have favoured articulation in the aboral direction (i.e. away from the oral surface). Thus, the feeding orientation of the crown may have been with the arms fanned out.

The interpretation of form and function of '*C.*' *ramosus* adopted herein has been largely determined by using modern isocrinids as a model. An attempt has been made to restore the possible life attitude of the column of '*C.*' *ramosus* (text-fig. 9) by functional interpretation and by comparison with living crinoids (e.g. Macurda and Meyer 1974, 1983). The proxistele, composed of numerous low columnals, was the most flexible part of the stem and would have enabled the crown to change orientation in response to changes in current direction (Pl. 72, figs. 1 and 2). Here there are two important factors to recognize. First, the life habit of '*C.*' *ramosus* in the high energy environment of a reef strongly implies that it was a rheophilic feeder (although the presence of abundant fenestrate bryozoans possibly suggests that energy levels in the reef environment were not always very high). This is reflected by the distribution of '*C.*' *ramosus* both laterally and vertically within different reef facies. Secondly, the crenularia of '*C.*' *ramosus* were radial, not petalloid as in isocrinids, so it was equally flexible in all directions through 360°. This was probably advantageous in making slight adjustments to changes in current direction. The mesistele lacked cirri, at least proximally, and probably functioned mainly to elevate the crown above the substrate, i.e. the height of elevation was approximately proportional to the length of the mesistele. Attachment was by the



TEXT-FIG. 9. Tentative restoration of the stem and crown of '*Cyathocrinites*' *ramosus* (Schlotheim) in life position, by analogy with modern isocrinids.

dististele, which was adapted as a cirriferous runner (compare Rasmussen 1977, fig. 2, with text-fig. 9 herein).

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